

CHECKLIST OF THE PARASITES OF CORAL REEF FISHES FROM FRENCH POLYNESIA, WITH CONSIDERATIONS ON THEIR POTENTIAL ROLE IN THESE FISH COMMUNITIES

by

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ABSTRACT. - The effects of parasites on coral reef fishes are largely unexplored and unknown. In other fish-parasite systems, parasites may have far reaching effects upon their hosts, leaving few aspects of their host's biology unaffected. In French Polynesia, coral reef fishes are relatively well studied, but the effects of parasites upon the coral reef fish communities there are unevaluated. As a first step, we conducted a survey of the macroparasites of coral reef fishes in French Polynesia. We found a diverse array of parasites infecting fishes, including cestodes, copepods, digeneans, isopods, monogeneans, and nematodes. Diversity of digeneans, the most common parasite group, was lower in French Polynesia than on the Great Barrier Reef. The majority (69%) of fishes examined were infected with at least one species of parasite. Finally, we discuss the potential of parasites to influence coral reef fish communities by altering host life histories, interspecific interactions, community structure, and larval dynamics.

RÉSUMÉ. - Inventaire des parasites des poissons des récifs coralliens de Polynésie Française, avec quelques considérations sur leur influence potentielle sur ces communautés de poissons.

Les effets des parasites sur les poissons des récifs coralliens sont largement ignorés et inconnus. Dans d'autres systèmes poissons-parasites, les parasites ont de tels effets qu'ils affectent la plupart des aspects de la biologie des hôtes. En Polynésie Française, les poissons des récifs coralliens sont relativement bien connus, mais les effets des parasites sur ces communautés de poissons n'ont pas été évalués. Dans un premier temps, nous avons dressé un inventaire des macroparasites des poissons coralliens et montré leur grande diversité: cestodes, copépodes, digènes, isopodes, monogènes et nématodes. La diversité des digènes, le groupe le plus commun de parasites, est plus faible en Polynésie Française que sur la Grande Barrière (Australie). La majorité des poissons examinés (69%) est infestée par au moins une espèce de parasite. Dans un deuxième temps, nous discutons de l'influence potentielle de ces parasites sur la communauté des poissons des récifs coralliens par l'altération des caractéristiques

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ques biologiques des hôtes, des interactions interspécifiques, de la structure des communautés et de la dynamique des larves de poissons.

Key-words. - Coral reef fishes, ISW, French Polynesia, Parasites, Checklist.

Parasites can generate selective pressure on their hosts that may have both short term ecological and long term evolutionary effects. In the short term, parasite virulence may modify the host's reproduction, growth, and mortality schedules as well as its competitive ability (reviewed in Price, 1980; Price *et al.*, 1986; Goater and Holmes, 1997). Over the long term, coevolution may lead to genetic changes in allele frequencies within the host population, affecting these and other life history traits to compensate for fitness losses from parasites (Michalakis and Hochberg, 1994) or defending against them. Given the above effects and the ubiquity of parasites, it is difficult to imagine examining the functioning of an ecosystem without considering the effects of parasites (Morand and Gonzalez, 1997). At present, there is a good body of literature on the ecology of coral reefs (e.g., Sale, 1991; Hixon and Beets, 1993; Sale *et al.*, 1994; Caley *et al.*, 1996; Hixon, 1997) and a large and developing literature on the systematics of the parasites of coral reef fishes (e.g., Lester and Sewell, 1989; Cribb *et al.*, 1994; Williams *et al.*, 1996). The role of coral reef fish parasites in the ecology and evolution of coral reef fish communities is largely unexplored. Recently however, this issue has begun to attract attention (Adlard and Lester, 1994). Nonetheless, our understanding of how parasites influence coral reef fish communities is still in its infancy.

As the coral reefs of French Polynesia have been intensively investigated (e.g., Dufour and Galzin, 1993; Galzin *et al.*, 1994; Planes *et al.*, 1996; Arias-Gonzalez *et al.*, 1997), it would seem to be a good place in which to attempt to integrate the role of parasites with our current understanding of the functioning of the coral reef ecosystem. Here, we present the results of a survey of the macroparasites of coral reef fishes in French Polynesia. We show that a substantial proportion of the fish population is infected by macroparasites. Our goal here is to stimulate interest among coral reef fish researchers. We therefore discuss how parasites may affect coral reef fish communities. We also identify possible model host-parasite systems for future investigation.

MATERIALS AND METHODS

Fish were collected by spear fishing and dissected while fresh. The gastrointestinal tract, other internal organs, and gills were examined for parasites under dissecting microscopes. Fixatives used were as follows: Hot 70% ethanol for nematodes, hot Bouin's fluid for digenleans, alcohol-formalin-acetic acid (AFA) for cestodes, and 70% ethanol for copepods and monogeneans. All parasites were preserved in 70% ethanol, 5% glycerin, and 1% phenol. Specimens were mounted and identified using standard procedures for the appropriate group. However, most monogeneans and copepods remain unidentified.

The program Chao2 estimator in the program EstiMateS (R.K. Colwell, unpubl.) was used to estimate the total number of digenlean families (see Colwell and Coddington, 1994; Walther and Morand, 1998) present in French Polynesian coral reef fishes based on our data and in Australian coral reef fishes based on unpubl. data from T.H. Cribb. This

removes the confounding effect of differences in sampling effort in each region, permitting statistical comparisons.

RESULTS

In May, 1995, we collected 189 fishes representing 72 species from 26 families from Moorea (Society Islands) and 74 fishes representing 40 species from 19 families from Rangiroa (Tuamotu Islands). We present the data as a host-parasite checklist for each island in the tables below (Tables I, II). Parasite species diversity is undoubtedly greater than given in the tables; i.e., as most parasites remain unidentified, some groupings may represent multiple species. We do not report the presence of larval parasites, except to note that encysted anisakid larvae and larval cestodes, *Scolex polymorphus*, were common in non-herbivorous coral reef fishes and uncommon in herbivorous fishes. Patterns in the parasites of *Cephalopholis argus*, *Dascyllus aruanus*, and *Stegastes nigricans* from Moorea are reported separately (Lo *et al.*, 1998; Lo *et al.*, 1999); camallanid nematodes of French Polynesian coral reef fishes are reviewed by Rigby (1999). Both studies include data not presented here.

Adult parasites were not found in the following fishes from Moorea: *Dendrochirus biocellatus* (1 examined), *Pterois radiata* (2), *Scorpaenodes guamensis* (2) (Scorpaenidae), *Scomberoides lysan* (1) (Carangidae), *Chaetodon trifasciatus* (8), *Forcipiger flavissimus* (1) (Chaetodontidae), *Centropyge bispinosus* (1) (Pomacanthidae), *Chromis atripectoralis* (1), *C. margaritifer* (1) (Pomacentridae), *Epibulus insidiator* (3), *Halichoeres hortulanus* (1), *Pseudocheilinus octotaenia* (1) (Labridae), *Aspidontis taeniatus* (1) (Blenniidae), *Canthigaster janthinoptera* (1), and *C. solandri* (1) (Tetraodontidae). Adult parasites were not found in the following fishes from Rangiroa: *Aulostomus chinensis* (1) (Aulostomidae), *Paracirrhites forsteri* (1) (Cirrhitidae), *Epibulus insidiator* (1) (Labridae), and *Valencienna strigatus* (1) (Gobiidae).

Juvenile cestodes (*Scolex polymorphus*) were common in coral reef fishes. Adult cestodes, however, were restricted to the Bothricephalidae, which we found infrequently in soldierfishes (Holocentridae), and the cestodes of sharks (Tables I, II). The Acanthocephala were also conspicuously absent. Similarly, on the Great Barrier Reef, adult cestodes are nearly absent and acanthocephalans are uncommon (Cribb *et al.*, 1994). Isopods, while rare on our checklists, are ectoparasites that do not generally occur in the parts of the fishes that we examined. Thus, their occurrence may be underestimated.

Among gill parasites, both monogeneans and copepods were common (infecting 36% and 15% of fishes examined, respectively). The monogeneans were dominated by a single family, Ancyrocephalidae. Exploration of patterns within both the monogeneans and copepods must await identification of the specimens, though these undoubtedly represent many species.

The Digenea were the most common adult gastro-intestinal parasites. They were represented by 15 families occurring in a wide range of hosts (Tables I, II). The estimated total number of digenetic families present in the coral reef fishes of French Polynesia is 16.5 ± 1.94 (s.e.) families. Further sampling in French Polynesia may thus be expected to reveal the presence of another 3-4 families of digenetics. In contrast, the estimated number of digenetic families present in coral reef fishes on the Great Barrier

Table I - Host-parasite checklist for the coral reef fishes of Moorea, Society Islands, French Polynesia. Parasite groups are as follows: gill parasites, Co = Copepoda, I = Isopoda and M = Monogenea; gastrointestinal parasites, C = Cestoda, D = Digenea and N = Nematoda. Intensity ranges with a "+" designate approximations or note the presence of a parasite. Relatively abundant fish species are shown in bold.

Fish family	Genus, species	N	Infected	Parasite group	Genera, species	Intensity range
Carcharhinidae	<i>Negaprion</i> sp.	1	1	C	<i>Phyllobothrium</i> sp.	3
			1		<i>Crossobothrium</i> sp.	3
			1		<i>Dicranobothrium</i> sp.	1
			1		<i>Dasyrhynchus</i> sp.	1
Muraenidae	<i>Gymnothorax undulatus</i>	1	1	D	Hemiuroid	3
			1		Bucephalid	18
Synodontidae	<i>Saurida gracilis</i>	2	1	M	Ancyrocephalid	1
			1		Hemiuroid	1
			1		<i>Spirocammallanus monotaxis</i>	4
Holocentridae	<i>Myripristis berndti</i>	4	1	C	Bothricephalid	1
			1			
	<i>M. violacea</i>	1	1	Co		1
			1			
	<i>Neoniphon opercularis</i>	1	1	Co		3
			1			
	<i>Sargocentron diadema</i>	11	1	M	Ancyrocephalid	4
			1		<i>Spirocammallanus monotaxis</i>	0
	<i>S. microstoma</i>	11	1	D	Bothricephalid	100+
			6		<i>Helicometra</i> sp.	1
	<i>S. spiniferum</i>	3	2	D	<i>Helicometra</i> sp.	2-15
			1		Ancyrocephalid	2-6
	<i>S. tiere</i>	3	1	M	Hemiuroid	3
			1		<i>Helicometra</i> sp.	3
			2		Ancyrocephalid	9
			2		Ancyrocephalid	6-7
Fistulariidae	<i>Fistularia commersonii</i>	1	1	Co		30+
			1		Bucephalid	3
			1		<i>Allolepidapedon petimba</i>	2
			1		<i>Neallolepidapedon hawaiiense</i>	1
Scorpaenidae	<i>Scorpaenopsis diabolus</i>	1	1	M	Ancyrocephalid	3
Serranidae	<i>Epinephelus fasciatus</i>	1	1	Co		3
			1		Ancyrocephalid	80+
			1		Capsalid	1
			1		<i>Bivesicula</i> sp.	17
	<i>E. merra</i>	1	1	D	Cyclopoid	
			1		<i>Lecithochirium</i> sp.	1
			1		<i>Philometra</i> sp.	1
Cirrhitidae	<i>Paracirrhites hemistictus</i>	1	1	M	Ancyrocephalid	100+
			1		<i>Bivesicula</i> sp.	1
Apogonidae	<i>Apogon fuscus</i>	2	1	N	<i>Spirocammallanus</i> sp. larva	1
			1		<i>Spirocammallanus</i> sp. larva	1
Polynemidae	<i>Polydactylus plebius</i>	1	1	D	Bucephalid	80
			1		<i>Spirocammallanus</i> sp. larva	1

Table I. – Continued.

Fish family	Genus, species	N	Infected	Parasite group	Genera, species	Intensity range
Carangidae	<i>Caranx melampygus</i>	2	2	M	Polyopisthocotylid	5-12
			1		Monopisthocotylid	4
			1	D	Bucephalid	25
	<i>Gnathanodon speciosus</i>	1	1	Co	Caligid	7
			1	M	Polyopisthocotylid	27
			1		Monopisthocotylid	1
			1	D	<i>Stephanostomum</i> sp.	1
			1		Bucephalid	31
Lutjanidae	<i>Lutjanus fulvus</i>	2	1	Co	Caligid	1
			2	M	Ancyrocephalid	15+
			1	D	<i>Hamacreadium mutabile</i>	1
	<i>Lutjanus gibbus</i>	2	1	Co	Caligid	3
			2	D	<i>Hamacreadium mutabile</i>	2-6
			1	N	<i>Cucullanus bourdini</i>	1
Lethrinidae	<i>Gnathodentex aureolineatus</i>	3	3	M	Ancyrocephalid	5-37
			3	N	<i>Spirocammallanus monotaxis</i>	3-10
	<i>Monotaxis grandoculis</i>	3	1	Co		1
			2	M	Ancyrocephalid	+
			1	D	<i>Propycnadenoides</i> sp.	2
			2	N	<i>Spirocammallanus monotaxis</i>	3-7
Mullidae	<i>Mulloidess flavolineatus</i>	5	4	M	Ancyrocephalid	1-14
			3	N	<i>Spirocammallanus istiblenni</i>	2-6
			2		Spirurid	6-6
			2	M	Ancyrocephalid	+
	<i>Parupeneus barberinus</i>	2	2	M	Ancyrocephalid	+
			1	M	Ancyrocephalid	+
			1	Co		3
			1	M	Ancyrocephalid	+
Chaetodontidae	<i>Chaetodon auriga</i>	4	4	M	Ancyrocephalid	4-100+
			1	Co		4
	<i>C. bennetti</i>	1	1	M	Ancyrocephalid	1
			1	M	Ancyrocephalid	26
	<i>C. citrinellus</i>	1	1	M	Ancyrocephalid	12
			1	M	<i>Neohypocreadium dorsoporum</i>	42
	<i>C. ornatissimus</i>	1	1	M	Ancyrocephalid	
			1	D		
Pomacanthidae	<i>Centropyge flavissimus</i>	17	2	D	Lecithasterid	1-2
			4	D	Monorchiid	1-23
	<i>Abudefduf sexfasciatus</i>	2	1	M	Ancyrocephalid	2
Pomacentridae	<i>Amphiprion chrysopterus</i>	1	1	Co	Cyclopoid	1
			1	N	<i>Spirocammallanus</i> sp.	1
Labridae	<i>Cheilinus chlorourus</i>	4	3	N	<i>Spirocammallanus monotaxis</i>	1-3
			1	D	Lecithasterid	1
	<i>Stethojulis bandanensis</i>	1	1	D	Lecithasterid	11
			1	N	<i>Camallanus</i> sp. larvae	2
	<i>Thalassoma hardwicke</i>	4	1	N	<i>Spirocammallanus</i> sp. larvae	1
			2		<i>Spirocammallanus monotaxis</i>	1-4

Table I—Continued 2.

Fish family	Genus, species	N	Infected	Parasite group	Genera, species	Intensity range
Pinguipedidae	<i>Parapercis millepunctata</i>	1	1	N	<i>Spirocammallanus monotaxis</i>	3
Acanthuridae	<i>Acanthurus guttatus</i>	1	1	M	Ancyrocephalid	27
			1	N	<i>Spirocammallanus colei</i>	2
	<i>A. lineatus</i>	2	2	M	Ancyrocephalid	9-20
			1	N	<i>Spirocammallanus colei</i>	3
	<i>A. nigrofasciatus</i>	1	1	Co		8
	<i>A. olivaceus</i>	1	1	M	Ancyrocephalid	12
			1	N	<i>Spirocammallanus chaimha</i>	2
	<i>Ctenochaetus striatus</i>	7	3	M	Ancyrocephalid	4-15
			4	N	<i>Spirocammallanus chaimha</i>	1-3
	<i>Naso lituratus</i>	2	1	D	<i>Preptetos</i> sp.	4
	<i>Zebrasoma scopas</i>	18	15	M	Ancyrocephalid	1-50+
			2		Dactylogyrid	30+
Bothidae	<i>Bothus mancus</i>	1	1	D	Hemirid	5
			1	N	<i>Spirocammallanus istiblenni</i>	5
Balistidae	<i>Balistapus undulatus</i>	3	1	Co		3
			1	D	<i>Helicometra</i> sp.	1
			3	N	<i>Cucullanus bourdini</i>	2-8
	<i>Rhinecanthus rectangulus</i>	1	1	D	<i>Macvicaria</i> sp.	9
	<i>Sufflamen bursa</i>	10	1	D	<i>Sphincterostoma</i> sp.	1
			1		<i>Hypocreadium</i> sp.	1
			3		<i>Macvicaria</i> sp.	1-10
			1	N	Ascarophid	1
			3		<i>Cucullanus</i> sp.	1
Ostraciidae	<i>Ostracion meleagris</i>	1	1	D	<i>Diploproctodaeum</i> sp.	2
Diodontidae	<i>Diodon hystrix</i>	2	2	Co		4-11
			2	D	<i>Maculifer</i> sp.	1-4
			1		<i>Opistholebes</i> sp.	2

Reef is 23.5 ± 1.12 families (based on a random sample of 295 fishes from T.H. Cribb's unpubl. data). Therefore, there is a lower diversity of digenean families in French Polynesian coral reef fishes than in coral reef fishes on the Great Barrier Reef (*t*-test, $t = 7.8651$, $p < 0.001$). Similarly, Rigby *et al.* (1997) reported that parasite species richness in the coral reef fish *Epinephelus merra* is lower in French Polynesia than on the Great Barrier Reef. Digeneans occurred in French Polynesia at the relatively low prevalence of 35% (disregarding age, length, habitat, and phylogenetic effects) in contrast to 70% on the Great Barrier Reef (Cribb *et al.*, 1994).

Adult nematodes were fairly common in French Polynesia (infecting 24% of fishes examined). The Camallanidae and Cucullanidae were the most common families (e.g., Morand and Rigby, 1998; Rigby, 1999). In a comparable survey of fishes from the Great Barrier Reef (Lester *et al.*, 1989), these groups did not occur as frequently.

The host-parasite systems which should prove to be the most amenable for field studies on the effects of parasites on their hosts are those in which the host is both common and regularly parasitized. This is largely a logistic concern; other systems may prove equally valuable for specific questions; e.g., a rare but highly virulent parasite may be equally rewarding to study. Relatively abundant fishes that appear to have a large parasite community in our limited samples are boxed in tables I and II.

The overall pattern that we found in French Polynesian parasites was that adult intestinal helminths were less common and less diverse when compared to other coral reef systems, as best illustrated in the comparison on the Digenea given above. The lower prevalence in French Polynesia than on the Great Barrier reef may be related to the great distance between small island populations. That is, the size and density of habitat patches are generally positively correlated with species richness and patch occupancy (Hanski, 1995; Rosenzweig, 1995). Thus, when host populations are small and separated, parasite species richness and prevalence may be low.

DISCUSSION

This study attempted to obtain a broad picture of which parasites were present in the coral reef fishes of French Polynesia and in what frequency they occurred. We found that fishes had a wide array of parasites (Tables I, II). Some common fishes were regularly parasitized, making them good candidates for future studies on the effects of parasites on their hosts (in bold in Tables I, II). Among the fishes examined, 69% were infected by parasites; 50% were infected by gastro-intestinal parasites and 47% by gill parasites. However, our study only surveyed the easily found macroparasites from 3 phyla. When microparasites and skin parasites are included, the parasites of fishes represent 9 phyla (not including bacteria or viruses) (Woo, 1995). Thus, with the high prevalence of macroparasites and the ubiquity of microparasites (especially bacteria), it is unlikely that many fishes escape parasitism at some point in their lives in French Polynesia. The effects of parasites on coral reef fishes remain largely unstudied. In what follows, we will briefly review the potential effects of parasites upon their hosts and relate those effects to coral reef fishes. We hope that this will stimulate coral reef fish researchers to consider the possible role of parasites in their study systems.

Many coral reef fishes have pelagic larval stages (Leis, 1991), which may be parasitized (Rigby and Dufour, 1996). While the effects of parasites on coral reef fish larvae have not been studied, parasites of other larval fishes may cause mortality, reduced growth, stamina, stress tolerance, energy reserves, and feeding ability (Williams and Jones, 1994). Models of coral reef fish communities have often stressed the importance of fish larvae in structuring adult fish communities (e.g., Sale, 1980; Victor, 1986; Doherty and Fowler, 1994) but do not consider the potential influence of parasites. Yet, the above effects may reduce the number of larvae recruiting to the reef by direct mortality, increased vulnerability to predation, or decreasing dispersal range. Additionally, the potentially lower condition of parasitized larvae recruiting to the reef may lead to a lower ability to persist on the reef with a subsequent impact on the adult fish community.

Table II. - Host-parasite checklist for the coral reef fishes of Rangiroa, Tuamotu Islands, French Polynesia. Parasite groups are as follows: gill parasites, Co = Copepoda, I = Isopoda and M = Monogenea; gastro-intestinal parasites, C = Cestoda, D = Digenea and N = Nematoda. Intensity ranges with a "+" designate approximations or note the presence of a parasite. Relatively abundant fish species are shown in bold.

Fish family	Genus, species	N	Infected	Parasite group	Genera, species	Intensity range
Carcharhinidae	<i>Negaprion</i> sp.	1	1	C	<i>Phoreiobothrium</i> sp.	3
Muraenidae	<i>Gymnothorax javanicus</i>	1	1	C	<i>Dicranobothrium</i> sp.	?
			1	D	<i>Orbitacolax</i> sp.	11
			1		<i>Hemiuroid</i>	20
			1		<i>Helicometra</i> sp.	1
			1		<i>Bucephalid</i>	14
Holocentridae	<i>Myripristis</i> kuhnee	4	3	Co	<i>Cucullanus</i> <i>faliexae</i>	28
			1	C	<i>Bothriocephalid</i>	1
			1	D	<i>Hemiuroid</i>	1
			1	N	<i>Cucullanus</i> <i>bourdini</i>	1
	<i>M. violacea</i>	1	1	Co		6
	<i>Sargocentron spiniferum</i>	3	1	Co		12
			2	D	<i>Hemiuroid</i>	3-5
			2	N	<i>Ascarophid</i>	1-30
Fistulariidae	<i>Fistularia commersonii</i>	1	1	D	<i>Neoallopelidapedon</i> <i>hawaiiense</i>	12
			1		<i>Hemiuroid</i>	1
			1		<i>Allopelidapedon</i> <i>petimba</i>	30
Serranidae	<i>Cephalopholis sexmaculata</i>	1	1	Co		3
	<i>C. urodelus</i>	1	1	Co		6
	<i>Epinephelus tauvina</i>	1	1	M	<i>Ancyrocephalid</i>	39
			1	D	<i>Hemiuroid</i>	1
	<i>Variola louti</i>	2	2	Co	<i>Hatschekia</i> sp.	2-6
			2	M	<i>Ancyrocephalid</i>	1-3
Priacanthidae	<i>Priacanthus cruentatus</i>	1	1	M	<i>Ancyrocephalid</i>	2
Lutjanidae	<i>Lutjanus bohar</i>	1	1	Co	<i>Hatschekia</i> sp.	6
			1	M	<i>Ancyrocephalid</i>	1
			1	D	<i>Cryptogonimid</i>	18
			1		<i>Hemiuroid</i>	1
			1		<i>Hamacreadium mutabile</i>	4
	<i>Lutjanus gibbus</i>	4	3	Co		1-7
			4	M	<i>Ancyrocephalid</i>	6-50+
			2	D	<i>Hemiuroid</i>	1-1
			1		<i>Helicometra</i> sp.	18
			1	N	<i>Spirurid</i>	4
Lethrinidae	<i>Lethrinus olivaceus</i>	4	4	M	<i>Cucullanus</i> <i>bourdini</i>	5
			1	D	<i>Spirocammallanus</i> sp.	1
			1			1-100+
			1			
			1	N	<i>Spirocammallanus</i> <i>monotaxis</i>	1
	<i>L. atkinsoni</i>	1	1	Co	<i>Lernanthropid</i>	1
	<i>Monotaxis grandoculis</i>	2	1	M	<i>Ancyrocephalid</i>	33
			2	N	<i>Spirocammallanus</i> <i>monotaxis</i>	3-9

Table II. – Continued.

Fish family	Genus, species	N	Infected	Parasite group	Genera, species	Intensity range
Mullidae	<i>Upeneus vittatus</i>	2	1 2	Co D	<i>Sagum</i> sp. Hemiuroid	1 1-15
Chaetodontidae	<i>Chaetodon lunula</i>	2	2	M	Ancyrocephalid	42-50+
	<i>C. ornatus</i>	1	1	M	Ancyrocephalid	50+
	<i>Heniochus monoceros</i>	2	2 1	Co N	<i>Hatschekia</i> sp. <i>Spirocammallanus</i> sp.	10-20 6
Labridae	<i>Cheilinus undulatus</i>	1	1 1 1 1	Co I M N	<i>Hatschekia napoleoni</i> Capsalid <i>Camallanus</i> sp.	100+ 1 50+ 1
Scaridae	<i>Scarus sordidus</i>	2	1	M	Ancyrocephalid	11
Blennidae	<i>Exallis brevis</i>	1	1	Co	Teaniachantid	9
Zanclidae	<i>Zanclus cornutus</i>	1	1	M	Ancyrocephalid	20+
Acanthuridae	<i>Acanthurus achilles</i>	2	1 1 2 2	Co M D N	Ancyrocephalid Angiodictyid <i>Spirocammallanus colei</i>	1 20 32-57 2-4
	<i>A. glaucopterus</i>	1	1	D	Glyiachenid	17
	<i>A. triostegus</i>	3	2 1	M N	Ancyrocephalid <i>Spirocammallanus colei</i>	15-44 1 3
	<i>Naso hexacanthus</i>	1	1 1	M D	Ancyrocephalid <i>Prosogonotrema</i> sp.	2-10 3
	<i>Zebrasoma rostratum</i>	3	3 1	M D	Ancyrocephalid Glyiachenid	4-13 2-8
	<i>Z. scopas</i>	6	6 2	M D	Ancyrocephalid <i>Schickhabalotrema</i> sp.	50-100+ 3
	<i>Z. veliferum</i>	4	4 1	M D	Ancyrocephalid <i>Prepitetus</i> sp.	1 2
Balistidae	<i>Balistapus undulatus</i>	2	1 1	Co N	<i>Hatschekia</i> sp. <i>Cucullanus bourdini</i>	2 3
	<i>Melichthys niger</i>	2	2 1 2	D	<i>Lepocreadium</i> sp. Hemiuroid Spirurid	5-5 1 2-7
	<i>Sufflamen bursa</i>	2	1 1	N	<i>Cucullanus</i> sp. <i>Spirocammallanus</i> sp.	1 1

The effects of parasites on adult coral reef fishes have so far been addressed in only one study. Adlard and Lester (1994) showed that when the coral reef fish *Chromis nitida* was infected with isopods, its growth, fecundity, and survival were lower than in uninfected fishes. The effects of the parasites that we found in the fishes of French Polynesian coral reef fishes (Tables I, II), though unstudied, should be similar to those of related parasites of fishes. Related parasites have many potential effects on fishes, including mortality, slowed growth, reduced energy reserves, swimming ability, weight, and repro-

duction (Williams *et al.*, 1994; Woo, 1995). Some microparasites may also suppress the host's immune system (Woo, 1995). The potential adverse effects of parasites on their individual hosts may translate to demographic or population level effects. For example, in simple systems, parasites may destabilise their host populations (Anderson and May, 1978; Hudson *et al.*, 1992). Parasites may also influence the outcome of interspecific interactions; e.g., highly parasitized species (or individuals) may lose out to those that are unparasitized or better able to cope with parasitism (Hudson and Greenman, 1998). Also, parasitized individuals may be more vulnerable to predation (Anderson, 1979).

The potential for coevolution or local adaptation in parasite-coral reef fish systems would seem low even though parasitism is common as 1) multiple species infections are common and 2) gene flow of both the host and the parasite may be high. Multiple species infections should increase the range of selective pressures to which the host may respond, potentially reducing the response to any one parasite; i.e., "diffuse coevolution" (Thompson, 1994). Both coral reef fishes and their parasites have pelagic larval stages (though this is not necessarily true for all parasites or fishes) (Leis, 1991; Marcogliese, 1995). Thus, both may have similar migration rates. When migration rates are similar and virulence is low, coevolution and local adaptation are unlikely (Gandon *et al.*, 1996; Lively, 1999). Yet, because some parasites may have high virulences, coevolution or local adaptation may still occur. Host species that have adapted to their parasites may have altered life histories. The most commonly reported response is alteration of the age at maturity (e.g., Boots and Begon, 1993; Lafferty, 1993; Langand *et al.*, 1998). In coral reef fishes, life history adaptations to parasites may be expressed as a change in larval duration, growth following recruitment, or body size. Body size may be most influenced by parasites that are positively correlated with host body size, as are some of the parasites that we found in French Polynesian fishes (Lo *et al.*, 1998).

Though the effects of the specific parasites we found in French Polynesian coral reef fishes have yet to be investigated, similar parasites of fishes express some degree of virulence (Williams *et al.*, 1994; Woo, 1995). Here, a sizable proportion of coral reef fishes were infected by macroparasites. We suggest that such widespread parasites may affect coral reef fish life histories, population and larval dynamics, and community structure. These effects may be the direct result of parasite pathology, the indirect result of parasite influence on interspecific interactions, or even the result of local adaptation or coevolution in fish host species. Undoubtedly, parasites have shaped coral reef ecosystems, but how and to what extent are questions that we hope will promote much new stimulating research.

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REFERENCES

ADLARD R.D. & R.J.G. LESTER, 1994. - Dynamics of the interaction between the parasitic isopod, *Anilocra pomacentri*, and the coral reef fish, *Chromis nitida*. *Parasitology*, 109: 311-324.

ANDERSON R.M., 1979. - The influence of parasitic infection on the dynamics of host population growth. In: *Population Dynamics* (May R.M., ed.), pp. 318-355. Oxford: Blackwell Scientific Publications.

ANDERSON R.M. & R.M. MAY, 1978. - Regulation of host-parasite population interactions: I. Regulatory processes. *J. Anim. Ecol.*, 47: 219-247.

ARIAS-GONZALEZ J.E., DELESCALE B., SALVAT B. & R. GALZIN, 1997. - Trophic functioning of the Tiahura reef sector, Moorea Island, French Polynesia. *Coral Reefs*, 16: 231-246.

BOOTS M. & M. BEGON, 1993. - Trade-offs with resistance to a granulosis virus in the Indian meal moth, examined a laboratory evolution experiment. *Funct. Ecol.*, 7: 528-534.

CALEY M.J., CARR M.H., HIXON M.A., HUGHES T.P., JONES G.P. & B.A. MENGE, 1996. - Recruitment and the local dynamics of open marine populations. In: *Annual Review of Ecology and Systematics* (Fautin D.G., ed.), pp. 477-500. Palo Alto: Annual Reviews.

COLWELL R.K. & J.A. CODDINGTON, 1994. - Estimating terrestrial biodiversity through extrapolation. *Phil. Trans. R. Soc. Lond. B, Biol. Sci.*, 345: 101-118.

CRIBB T.H., BRAY R.A., BARKER S.C., ADLARD R.D. & G.R. ANDERSON, 1994. - Ecology and diversity of digenetic trematodes of reef and inshore fishes of Queensland. *Int. J. Parasitol.*, 24: 851-860.

DOHERTY P.J. & A.J. FOWLER, 1994. - An empirical test of recruitment limitation in a coral reef fish on the Great Barrier Reef. *Science*, 263: 935-939.

DUFOUR V. & R. GALZIN, 1993. - Colonization patterns of reef fish larvae to the lagoon at Moorea Island, French Polynesia. *Mar. Ecol. Progress Ser.*, 102: 143-152.

GALZIN R., PLANES S., DUFOUR V. & B. SALVAT, 1994. - Variation in diversity of coral reef fish between French Polynesian atolls. *Coral Reefs*, 13: 175-180.

GANDON S., CAPOWIEZ Y., DUBOIS Y., MICHALAKIS Y. & I. OLIVIERI, 1996. - Local adaptation and gene-for-gene coevolution in a metapopulation model. *Proc. R. Soc. Lond. Ser. B, Biol. Sci.*, 263: 1003-1009.

GOATER C.P. & J.C. HOLMES, 1997. - Parasite-mediated natural selection. In: *Host-Parasite Evolution: General Principles and Avian Models* (Clayton D.H. & J. Moore, ed.), pp. 9-29. Oxford: Oxford Univ. Press.

HANSKI I., 1995. - Metapopulation dynamics: From concepts and observations to predictive models. In: *Metapopulation Biology: Ecology, Genetics and Evolution* (Hanski I. & M.E. Gilpin, eds), pp. 69-91. San Diego: Academic Press.

HIXON M.A., 1997. - Effects of reef fishes on corals and algae. In: *Life and Death of Coral Reefs* (Birkeland C., ed.), pp. 230-248. New York: Chapman and Hall, Inc.

HIXON M.A. & J.P. BEETS, 1993. - Predation prey refuges and the structure of coral-reef fish assemblages. *Ecol. Monogr.*, 63: 77-101.

HUDSON P.J. & J. GREENMAN, 1998. - Competition mediated by parasites: Biological and theoretical progress. *Trends Ecol. Evol.*, 13: 387-390.

HUDSON P.J., NEWBORN D. & A.P. DOBSON, 1992. - Regulation and stability of a free-living host-parasite system: *Trichostrongylus tenuis* in red grouse. I. Monitoring and parasite reduction experiments. *J. Anim. Ecol.*, 61: 477-486.

LAFFERTY K.D., 1993. - The marine snail *Cerithidea californica* matures at smaller sizes where parasitism is high. *Oikos*, 68: 3-11.

LANGAND J., JOURDANE J., COUSTAU C., DELAY B. & S. MORAND, 1998. - Cost of resistance, expressed as a delayed maturity, detected in the host-parasite system *Biomphalaria glabrata-Echinostoma caproni*. *Heredity*, 80: 320-325.

LEIS J.M., 1991. - The pelagic stage of reef fishes: The larval biology of coral reef fishes. In: *The Ecology of Fishes on Coral Reefs* (Sale P.F., ed.), pp. 183-230. San Diego: Academic Press.

LESTER R.J.G. & K.B. SEWELL, 1989. - Checklist of parasites from Heron Island, Great Barrier Reef (Australia). *Aust. J. Zool.*, 37: 101-128.

LIVELY C.M., 1999. - Migration, virulence, and the geographic mosaic of adaptation by parasites. *Am. Nat.*, 153: S34-S47.

LO C.M., MORAND S. & R. GALZIN, 1998. - Parasite diversity/host age and size relationship in three coral reef fishes from French Polynesia. *Int. J. Parasitol.*, 28: 1695-1708.

LO C.M., MORAND S. & R. GALZIN, 1999. - The parasitism of coral reef fish. Reflection of habitat? *C.R. Acad. Sci., Ser. III, Sci. Vie*, 322: 281-287.

MARCOGLIESE D.J., 1995. - The role of zooplankton in the transmission of helminth parasites to fish. *Rev. Fish Biol. Fish.*, 5: 336-371.

MICHALAKIS Y. & M.E. HOCHBERG, 1994. - Parasitic effects on host life-history traits: A review of recent studies. *Parasite*, 1: 291-294.

MORAND S. & E.A. GONZALEZ, 1997. - Is parasitism a missing ingredient in model ecosystems? *Ecol. Model.*, 95: 61-74.

MORAND S. & M.C. RIGBY, 1998. - Cucullanin nematodes from coral reef fishes of French Polynesia, with a description of *Cucullanus faliexae* n. sp. (Nematoda: Chitwoodchabaudiidae). *J. Parasitol.*, 84: 1213-1217.

PLANES S., GALZIN R. & F. BONHOMME, 1996. - A genetic metapopulation model for reef fishes in oceanic islands: The case of the surgeonfish, *Acanthurus triostegus*. *J. Evol. Biol.*, 9: 103-117.

PRICE P.W., 1980. - Evolutionary Biology of Parasites. 237 p. Princeton: Princeton Univ. Press.

PRICE P.W., WESTOBY M., RICE B., ATSTATT P.R., FRITZ R.S., THOMPSON J.N. & K. MOBLEY, 1986. - Parasite mediation in ecological interactions. *Ann. Rev. Ecol. Syst.*, 17: 487-505.

RIGBY M.C., 1999. - The Camallanidae (Nematoda) of Indo-Pacific fishes: Taxonomy, ecology, and host-parasite coevolution. In: Proc. 5th Indo.-Pac. Fish Conf., Nouméa, 1997 (Séret B. & J.-Y. Sire, eds), pp. 633-644. Paris: Société Française d'Ictyologie (SFI) & Institut de Recherche pour le Développement (IRD).

RIGBY M.C. & V. DUFOUR, 1996. - Parasites of coral reef fish recruits, *Epinephelus merra* (Serranidae), in French Polynesia. *J. Parasitol.*, 82: 405-408.

RIGBY M.C., HOLMES J.C., CRIBB T.H. & S. MORAND, 1997. - Patterns of species diversity in the gastrointestinal helminths of a coral reef fish, *Epinephelus merra* (Serranidae), from French Polynesia and the South Pacific Ocean. *Can. J. Zool.*, 75: 1818-1827.

ROSENZWEIG M.L., 1995. - Species Diversity in Space and Time. 436 p. Cambridge: Cambridge Univ. Press.

SALE P.F., 1980. - The ecology of fishes on coral reefs. *Oceanogr. Mar. Biol. Ann. Rev.*, 18: 367-421.

SALE P.F., 1991. - The Ecology of Fishes on Coral Reefs. 754 p. San Diego: Academic Press.

SALE P.F., GUY J.A. & W.J. STEEL, 1994. - Ecological structure of assemblages of coral reef fishes on isolated patch reefs. *Oecologia*, 98: 83-99.

THOMPSON J.N., 1994. - The Coevolutionary Process. 376 p. Chicago: Univ. of Chicago Press.

VICTOR B.C., 1986. - Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. *Ecol. Monogr.*, 56: 145-160.

WALTHER B.A. & S. MORAND, 1998. - Comparative performance of species richness estimation methods. *Parasitology*, 116: 395-405.

WILLIAMS E.H. Jr., BUNKLEY-WILLIAMS L. & W.G. DYER, 1996. - Metazoan parasites of some Okinawan coral reef fishes with a general comparison to the parasites on Caribbean coral reef fishes. *Galaxea*, 13: 1-13.

WILLIAMS H.H. & A. JONES, 1994. - Parasitic Worms of Fish. 593 p. London: Taylor and Francis.

WOO P.T.K., 1995. - Fish Diseases and Disorders. 808 p. Wallingford (UK): CAB International.

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